

Consistency in the behaviour types of the Atlantic cod: repeatability, timing of migration and geo-location

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ABSTRACT: We investigated the behaviour patterns of coastal (relatively stationary in shallow waters) and migratory frontal (offshore) types of Atlantic cod *Gadus morhua* in Icelandic waters using information from data storage tags (DSTs). Consistent and repeated patterns of migration were observed for both coastal and frontal cod, with characteristic DST profiles repeated from year to year. The migration timing in 2 successive years was close to being synchronous, suggesting that the onset of migration was consistent from year to year. A tidal location model suggested that the feeding migrations of cod in Icelandic waters were undertaken in groups or shoals during the whole year. The overall stability of the behaviour patterns of both types suggests that coastal and frontal individuals use different behavioural strategies which might either be related to food availability/competition or genetic control.

KEY WORDS: *Gadus morhua* · Iceland · Behaviour types · Seasonality · Feeding strategies

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INTRODUCTION

Seasonal variations in the environment, and consequently variations in food supplies, continuously induce annual migrations of most species in birds, mammals or fishes over short or vast distances. Due to the development of promising tracking methods, migration studies have been flourishing in recent decades, with particular emphasis on multiple year patterns (Egevang et al. 2010, Klaassen et al. 2011, Matthews et al. 2011, Olifiers et al. 2011, Vardanis et al. 2011, Forsythe et al. 2012). In this context, data storage tags (DSTs) allow the investigation of thermo-bathymetric migration patterns of fish, and the variability of individual migrations, using relatively long-term storage DSTs (Neat et al. 2006). In Atlantic cod *Gadus morhua* L., individual behaviour

related to feeding migrations has been shown to vary within a single spawning ground. Two behaviour types have been observed, i.e. a coastal, relatively stationary type in shallow waters, and a migratory frontal (offshore) type, breeding in shallow waters but migrating to deeper waters to commonly feed near thermal fronts (Nordeide 1998, Godo & Michalsen 2000, Pálsson & Thorsteinsson 2003, Neat et al. 2006). Both behaviour types have been studied in Norwegian (Nordeide 1998, Godo & Michalsen 2000) and Icelandic waters (Pálsson & Thorsteinsson 2003, Pampoulie et al. 2008a), and have been shown to segregate by depth both during spawning and feeding time (Nordeide 1998, Grabowski et al. 2011). Recent studies have also shown genotype differences at the pantophysin locus (*Pan I*, see Fevolden & Pogson 1997, Sarvas & Fevolden 2005, Skarstein et al. 2007,

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Pampoulie et al. 2008a). The pantophysin *Pan* I^B allele was predominantly observed in northeast Arctic cod and in the Icelandic frontal type, while the *Pan* I^A allele was predominantly observed in Norwegian coastal cod and in the Icelandic coastal type. However, despite intensive research on these 2 behaviour types, no studies have dealt with year-to-year repeatability of individual migrations, or the timing and routes of migrations. This information can be retrieved from DSTs (Hunter et al. 2004, Metcalfe 2006) and may shed new light on feeding migration processes (i.e. whether individuals move in groups/shoals) and on the consistency of the migration habits of these behaviours.

We investigated the thermo-bathymetric migration patterns of the coastal and frontal behaviour types of Atlantic cod in Icelandic waters. Our main goal was to evaluate the repeatability of individual migration patterns and the timing of migrations within and between behaviour types. An attempt at geo-location of individuals of both behaviour types to assess whether individuals move in groups or shoals was also performed.

MATERIALS AND METHODS

The DSTs used were DSTmilli and DSTcenti-ex, produced by Star Oddi, and their characteristics were already described (Pampoulie et al. 2008a). The DSTcenti-ex recorded temperature and depth every

10 min during the first 2 yr. To extend the sampling time through the third year, the tags were set to a measuring frequency of 6 h, except in April and October. The tagging procedure is fully described on the following web site: www.hafro.is/skrar/flokkar/merkingar_thorskur.pdf.

During the years 2002 to 2005, 1104 cod were tagged and released with DSTs in Icelandic waters; of these, 347 (31.4%) were recaptured up to 1807 d later. Tagging localities at the southwest (SW), southeast (SE), west (W) and northeast coasts (NE) of Iceland were selected for the study (Fig. 1). Spawning cod, 65 to 107 cm in length, were captured using gillnets off the southern and western coasts and by Danish seine off the NE coast.

Seasonality and timing of migration

In total, 41 DST-tagged fish were recaptured at least 18 mo after release and were used for the analysis of temporal stability and repetitive behaviour (Supplement 1 at www.int-res.com/articles/suppl/m462p251_supp.pdf). The classification of behaviour types as coastal versus frontal was performed according to previous studies (Pálsson & Thorsteinsson 2003, Pampoulie et al. 2008a, Grabowski et al. 2011). In general, coastal and frontal behaviours were defined according to the annual temperature and depth history of the tagged individuals. Coastal types (C) spend at least 70% of their time in shallow waters showing an annual rise in temperature to a maximum in September/October and decline in temperature to a minimum in February/March. The frontal types (F) share the depth range of the coastal types during spawning migrations, but during feeding migrations, they move to deeper waters (250 to 600 m). The temperature history showed visits to thermal fronts and frequent vertical migrations moving between extremes in temperatures typically found at such locations (<0°C and >7°C).

The temporal stability in depth and temperature profiles between years of each individual was estimated with Pearson correlation between monthly mean depth and temperature of a particular month in 2 consecutive years. Between-year consistency in timing of arrival at, and departure

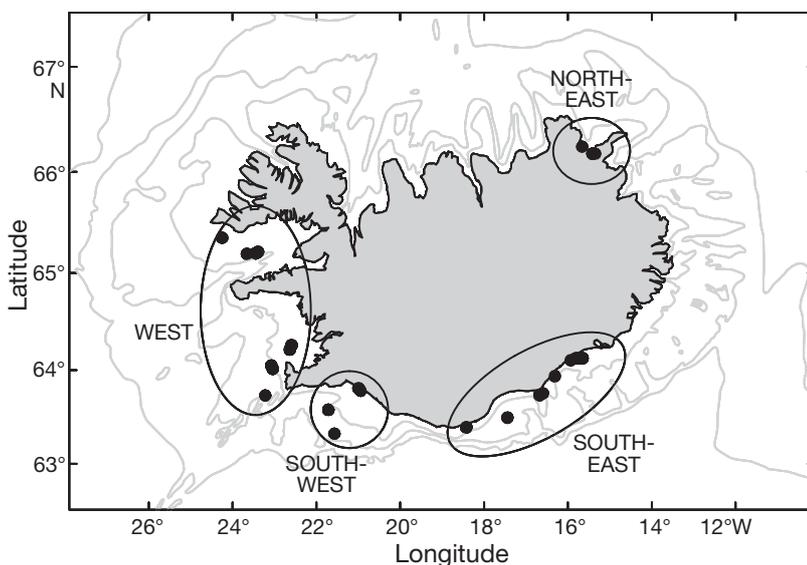


Fig. 1. *Gadus morhua*. Release areas of adult cod with data storage tags on spawning grounds in 2003 to 2005 that were recaptured after at least 18 mo. Depth contours at 100, 200, 500 m

from, a spawning ground was tested with analysis of covariance (ANCOVA), with time of migration in the latter year as the dependent variable, time of migration in the former year as a covariate and behaviour type as a random factor. The model is expressed as:

$$T = \beta_0 + \beta_1 \times T_{y+1} + \beta_2 \times M + \beta_3 (T_{y+1} \times M) + \varepsilon \quad (1)$$

where T is the day of the year in the former year, T_{y+1} is the day of the year in the latter year, M is the behaviour type, β_0 is the intercept, β_1 , β_2 are the slopes for the 2 variables, β_3 is the slope for the interaction term, and ε is the error term. Timing of arrival and departure was estimated from the behaviour pattern as day of the year. Individual cod are found at lower depths on the spawning grounds than during the feeding migrations. Therefore, patterns are easily seen in the depth profiles (Fig. 2), and the time of arrival on the spawning ground can be estimated from the vertical activity. Periods of low vertical activity, when cod are found at the same depth for more than 2 d at the end of the migratory period, are characteristic of individuals arriving at the spawning ground. During the following period of low activity, the cod remain at the spawning ground. When the

behaviour pattern reverts to increased vertical activity, and the cod moves into deeper waters, the fish has left the spawning ground. Eight comparisons of each behaviour type were included in the model, as migration from and to the spawning ground could only be compared using 8 coastal and 8 frontal individuals. Behaviour type was not significant and was removed from the final model for simplification. The new model was expressed as:

$$T = \beta_0 + \beta_1 \times T_{y+1} + \varepsilon \quad (2)$$

Estimating location from a tidal model

The tidal model location was applied to the 41 DSTs retrieved more than 18 mo after release. Measurements of frequency of 6 h were omitted due to insufficient temporal resolution to detect the tidal oscillation, and the limit was therefore set at 10 min. Furthermore, the fish must stay at the seafloor (at a constant depth), during several hours to cover the tidal wave. A data base of amplitude and phase of 7 tidal harmonic constituents on a 0.25° longitude and 0.10° latitude grid was used as a basis for the tidal

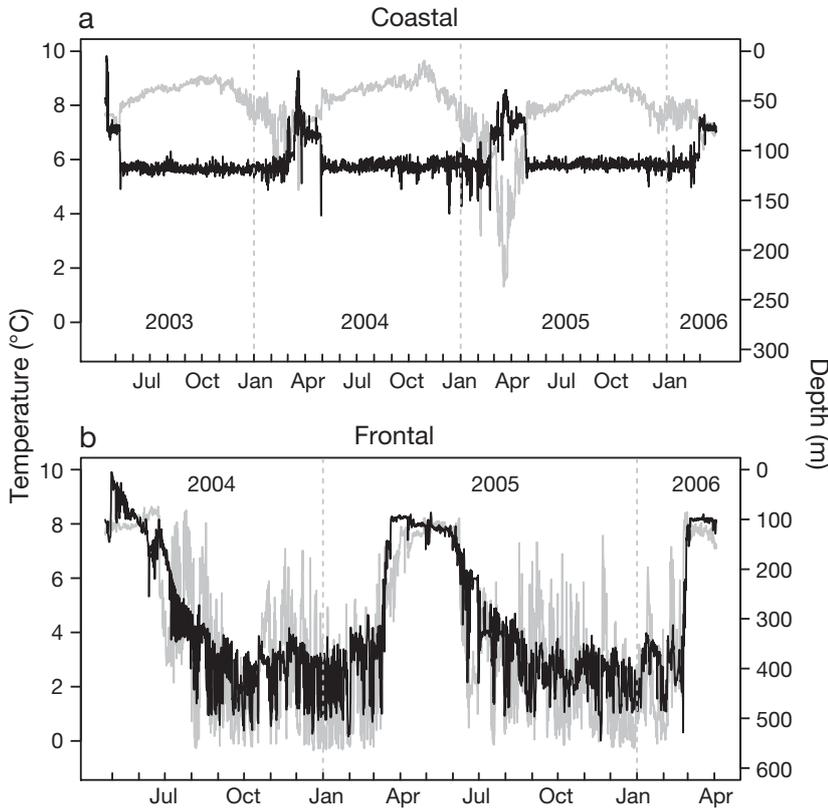


Fig. 2. *Gadus morhua*. Typical (a) coastal and (b) frontal data storage tag profiles over more than 2 yr. Depth = black line, temperature = grey line

location of the fish. The data originated from a numerical model of the tides in the North Atlantic Ocean around Iceland, developed by Tómasson & Káradóttir (2005). The model extends over an area of 5.7×10^6 km² with 10×10 km resolution over the whole model domain but 2×2 km resolution on the Icelandic shelf. It is based on 7 tidal harmonic constituents and takes boundary conditions at open ocean boundaries from a larger global model (Finite Element Solution, FES 2004; www.avisoocean.com/en/data/products/auxiliary-products/global-tide-fes2004-fes99/description-fes2004/index.html). The model has been calibrated and verified extensively with data from harbours and mooring stations around Iceland and elsewhere. Its accuracy on the Icelandic shelf is within a few centimetres in amplitude and a few minutes in phase. The tidal location method used here is an extension of that presented by Pedersen et al. (2008). The first step is to search the entire data series for possible tidal patterns. A tidal pattern is identified

where fitting to a sine curve over a sliding window of 10 h in length satisfies 3 criteria, i.e. root mean square error (RMSE) < 0.42 m, coefficient of determination $R^2 > 0.85$ and amplitude of the fitted sine wave $A > 0.3$ m. The second step, applied when a fit to a sine curve is identified, consists of finding the most probable location of the fish by comparison of the amplitude and phase of the fitted sine curve with calculated tidal signals within the model domain. These steps are identical to those of Pedersen et al. (2008) (except for the criteria on minimum amplitude, which were twice as small in this study to adapt to tidal conditions in the sea around Iceland) resulting in an automatically proposed location of the fish. However, those criteria alone were found to propose too many false or unreliable tidal signals and locations when applied to data from Icelandic cod. Therefore, a third step was added based on the visual comparison of observed tidal DST-pattern of the cod and the modelled tidal oscillation at the predicted location. Based on a comparative evaluation of the agreement between the 2, and an inspection of other possible tidal patterns in nearby time intervals, taking into account cod swimming speed and distance from the last accepted location, a final decision was made on acceptance or rejection of the tidal location. With this additional step, around one-third of the originally proposed tidal patterns and locations were rejected. A more detailed description of the methodology used is given and supported with examples from analysis of the DST pattern of a cod with the tag identification number (tag ID) 2C0645 (Supplement 2 at www.int-res.com/articles/suppl/m462p251_supp.pdf). The accuracy and reliability of the predicted tidal locations was verified by applying the method to time series from stationary tags (tags moored at fixed locations). The results showed that if a signal was correctly identified as a tidal signal, the predicted location was reliable with an accuracy of 10 to 20 km in most cases (see Supplement 3 at www.int-res.com/articles/suppl/m462p251_supp.pdf for results of the verification).

RESULTS

Seasonality

Data retrieved from the 41 individual DSTs revealed a high degree of inter-annual regularity in temperature and depth patterns, with a typical pattern of coastal cod inhabiting the same depths and temperatures during 3 yr (Fig. 2) and a typical pattern of frontal cod visiting the same depths over a

period of 2 yr at low and fluctuating temperatures, and returning to shallower water at a fairly constant time of the year (Fig. 2).

The 2 behaviour types clearly displayed distinct seasonal patterns of temperature and depth (Figs. 2 & 3), and individuals of both types retained their behaviour characteristics through the observation time, i.e. coastal behaviour types did not demonstrate frontal behaviour patterns or vice versa. The annual temperature patterns of coastal cod were characterised by typical sinusoidal curves in all areas with minimum values during the spawning season and maximum values in autumn. The temperature pattern of coastal cod was fairly uniform in the southern areas and not different from the mean, but lower in the NE area (Fig. 3e,g). Similarly, the period of minimum temperatures lasted longer in the NE area than in the south. The annual temperature patterns of frontal cod in the southern areas were basically reversed to that of coastal cod, with maximum temperatures during the spawning season, but minimum temperatures during the feeding season. The patterns were not different among the 3 investigated areas (Fig. 3f). In the southern areas, the temperatures of frontal cod declined abruptly after the spawning season to a minimum level until late autumn or winter. At the same time, variability (first and third quantiles) in temperature and depth increased substantially indicating foraging activity at thermal fronts. In the NE area, however, the annual temperature patterns were similar between the 2 behaviours, with maximum values in autumn, but lower values were observed in the frontal group. However, increased temperature range was seen in the frontal group in the NE area from June through November, indicating increased activity at thermal fronts (Fig. 3g,h).

The depth patterns of coastal cod showed largely similar trends across areas with shallowest distributions in April at the time of peak spawning, although the depth pattern in the NE area was shallower (Fig. 3a,c). The observed depth distribution patterns of frontal cod were more highly pronounced than for the coastal type, showing clear migrations into shallower waters during the spawning season in March and April, followed by migrations into deeper waters, associated with increased variability in depth, and reaching maximum depths in autumn (Fig. 3b,d). The frontal cod in the NE area inhabited shallower waters than frontal cod in the other areas in all months (Fig. 3d). The temperature and depth patterns of the coastal and frontal behaviours indicate considerable separation during feeding migrations, but similar habitats during the spawning season in February to

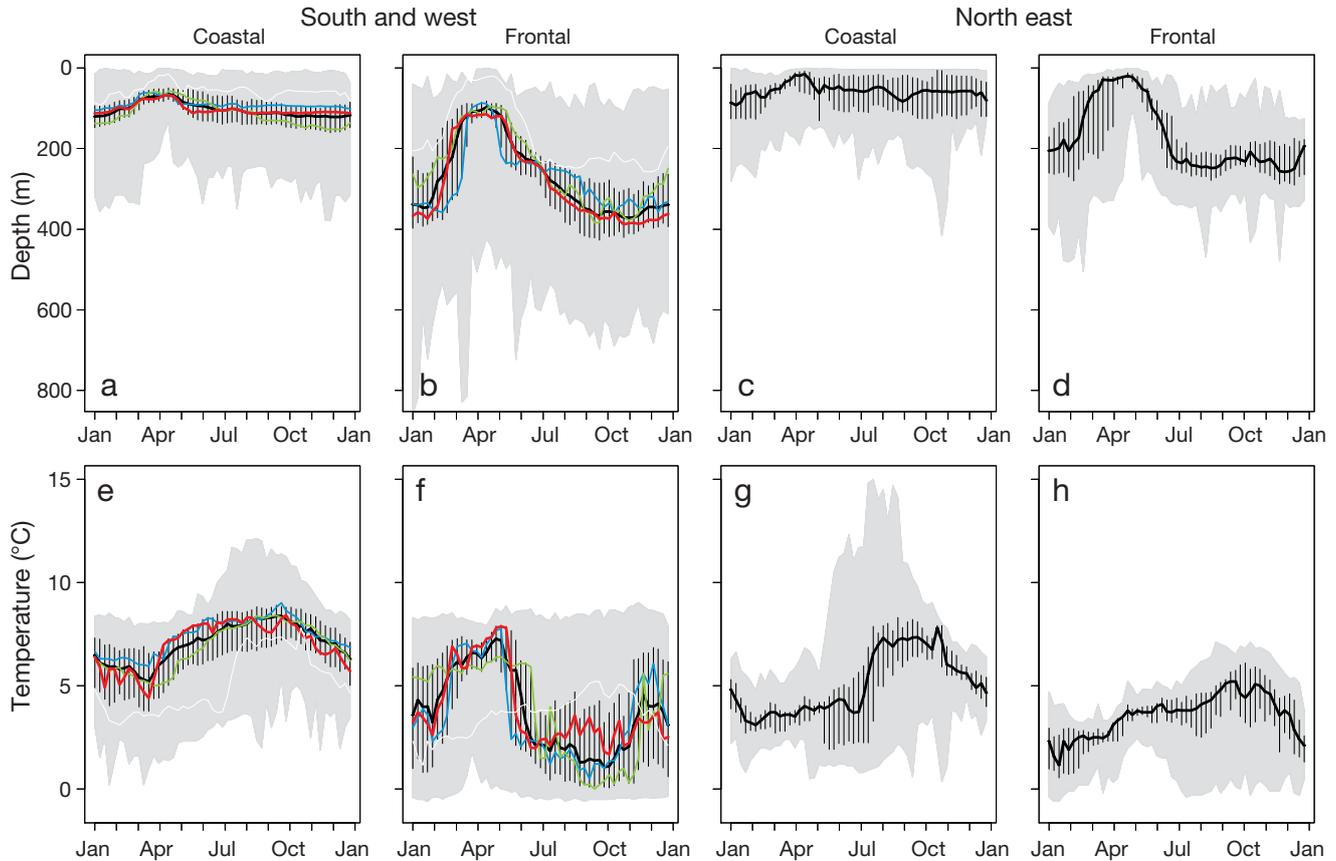


Fig. 3. *Gadus morhua*. Weekly depth and temperature profiles (median \pm first and third quartiles) for (a, c, e, g) coastal and (b, d, f, h) frontal cod. Grey shading shows weekly minimum and maximum depth and temperature. South west (red), south east (blue), west (green), north east (white in a, b, e, f, black in c, d, g, h) and combined south and west areas (black in a, b, e, f)

May when sexually mature fish of both behaviour types are located in coastal waters. In addition, the comparison of migration patterns of both behaviours showed that individuals consistently occupied similar depth/temperature niches during the same month in consecutive years (Table 1). Only 4 out of 53 comparisons were not correlated in mean monthly temperature and depth between 2 consecutive years (Table 1). Exception to the high degree of inter-annual regularity were also observed (Table 1), such as 2 frontal cod (tag ID 1C0480 and 1C1477) which showed typical behaviour patterns except in spawning time, where they appeared to have skipped spawning.

Timing of migration

Individuals of both behaviour types arrived at the spawning grounds around mid-March and left for the feeding grounds at various times from the end of May to the end of June. Although based on a relatively small number of samples ($n = 8$ for each behaviour),

the arrival on the spawning ground in the second year was significantly related to that of the first year (ANCOVA; $F = 5.274$; $p = 0.038$). No significant differences could be observed between dates of arrival at spawning grounds of the behaviour types. Likewise, the departure from the spawning ground in the second year was significantly related to departure in the first year (ANCOVA; $F = 6.312$; $p = 0.0249$), and no differences were observed between behaviour types.

Geo-location and shoal migration

Geographic positions of 2 coastal individuals tagged at similar locations (Fig. 4) showed that they stayed within the same bay during the 2 yr time series. The tidal model furthermore showed that coastal individuals were repeatedly found close to each other (10 to 20 km) during 3 seasons (Fig. 5), which tends to confirm that they moved together in a concurrent way and exhibited fidelity to migrating routes, areas and groups or shoals. The tidal location

Table 1. *Gadus morhua*. Pearson's correlation between mean depth (r_d) and mean temperature (r_t) of a particular month and the same month in the following year for (a) coastal and (b) offshore cod (recapture after at least 18 mo). The period from April to March in 2 consecutive years was compared. In cases where recaptures were earlier, the period from April to the time of recapture was compared (September to February). Tag ID: data storage tag identification. df: degrees of freedom; p: p values for mean depth (p_d) and mean temperature (p_t); **bold** values indicate significance at $\alpha = 0.05$

Tag ID	df	r_d	p_d	r_t	p_t	Periods compared
a) Coastal cod						
3C0306	10	0.52	0.084	0.79	<0.001	2005/2006 and 2006/2007
2C0378	10	0.85	<0.001	0.84	<0.001	2005/2006 and 2006/2007
2C0378	4	0.91	<0.001	0.99	<0.001	2006 and 2007
1C0397	10	0.006	0.985	0.82	0.001	2003/2004 and 2004/2005
1C0397	9	0.31	0.356	0.83	0.001	2004/2005 and 2005/2006
2C0404	10	0.76	0.004	0.89	<0.001	2005/2006 and 2006/2007
1C0407	10	0.95	<0.001	0.79	0.002	2003/2004 and 2004/2005
1C0407	10	0.98	<0.001	0.62	0.030	2004/2005 and 2005/2006
2C0417	10	0.90	<0.001	0.86	<0.001	2003/2004 and 2004/2005
2C0417	10	0.97	<0.001	0.56	0.060	2004/2005 and 2005/2006
1C0431	4	0.42	0.408	0.94	0.005	2003 and 2004
1C0444	10	0.87	<0.001	0.96	<0.001	2003/2004 and 2004/2005
1C0503	6	0.85	0.008	0.90	0.003	2003 and 2004
2C1517	10	0.75	0.005	0.81	0.001	2005/2006 and 2006/2007
2C0641	5	0.35	0.440	0.99	<0.001	2004 and 2005
2C0645	5	0.45	0.308	0.84	0.018	2004 and 2005
3C0650	4	-0.60	0.206	0.95	0.004	2004 and 2005
1C1166	10	0.37	0.239	0.92	<0.001	2004/2005 and 2005/2006
1C1166	10	0.56	0.058	0.83	<0.001	2005/2006 and 2006/2007
1C1195	9	0.97	<0.001	0.75	0.008	2004/2005 and 2005/2006
1C1224	6	0.01	0.975	0.62	0.104	2004 and 2005
1C1225	10	-0.12	0.695	0.23	0.462	2003/2004 and 2004/2005
1C1231	4	-0.49	0.328	0.84	0.038	2004 and 2005
1C1240	10	0.78	0.003	0.49	0.104	2004/2005 and 2005/2006
1C1282	8	0.9	<0.001	0.50	0.146	2004/2005 and 2005/2006
2C1489	10	0.87	<0.001	0.94	<0.001	2005/2006 and 2006/2007
b) Frontal cod						
2C0426	10	0.77	0.003	0.88	<0.001	2005/2006 and 2006/2007
2C0444	10	0.39	0.262	0.66	0.039	2005/2006 and 2006/2007
1C0480	10	0.06	0.849	-0.04	0.907	2003/2004 and 2004/2005
2C0544	10	0.92	<0.001	0.83	<0.001	2003/2004 and 2004/2005
2C0544	10	0.86	<0.001	0.85	<0.001	2004/2005 and 2005/2006
1C0585	10	0.89	<0.001	0.80	0.002	2003/2004 and 2004/2005
1C0585	10	0.93	<0.001	0.57	0.053	2004/2005 and 2005/2006
1C0593	10	0.75	0.005	0.52	0.081	2003/2004 and 2004/2005
1C0595	10	0.84	<0.001	0.95	<0.001	2003/2004 and 2004/2005
1C0605	10	0.76	0.004	0.85	<0.001	2003/2004 and 2004/2005
1C0611	10	0.92	<0.001	0.88	<0.001	2003/2004 and 2004/2005
1C0611	9	0.67	0.024	0.55	0.082	2004/2005 and 2005/2006
2C0669	10	0.72	0.008	0.88	<0.001	2004/2005 and 2005/2006
1C1198	8	0.91	<0.001	0.97	<0.001	2004/2005 and 2005/2006
1C1146	10	0.46	0.133	0.68	0.014	2003/2004 and 2004/2005
1C1146	10	0.54	0.067	0.74	0.006	2004/2005 and 2005/2006
1C1164	10	0.83	<0.001	0.83	<0.001	2004/2005 and 2005/2006
1C1164	10	0.88	<0.001	0.80	<0.001	2005/2006 and 2006/2007
1C1244	4	0.99	<0.001	0.53	0.283	2004 and 2005
1C1426	10	0.74	0.006	0.69	0.013	2004/2005 and 2005/2006
1C1448	10	0.93	<0.001	0.78	0.003	2004/2005 and 2005/2006
1C1477	10	-0.43	0.164	-0.45	0.138	2004/2005 and 2005/2006
1C1480	10	0.84	<0.001	0.44	0.157	2004/2005 and 2005/2006
1C1480	10	0.97	<0.001	0.80	0.002	2005/2006 and 2006/2007
2C1492	10	0.83	<0.001	0.77	0.003	2005/2006 and 2006/2007
3C1499	10	0.84	<0.001	0.79	0.002	2005/2006 and 2006/2007
3C1499	3	0.90	0.036	0.98	0.004	2006 and 2007

data including all recovered DSTs (Fig. 5) also showed that during spawning time and spawning migrations (February to May), individuals of each behaviour type were distributed in the same area, but frontal cod occupied deeper parts of the spawning grounds compared to the coastal cod. In the summer (June to September) and winter feeding migrations (October to January) the distributions were uneven, as coastal cod were more prominent in shallow waters in the south, SW and SE. Frontal cod were mostly found in deeper waters in the north, NW and NE, where they were likely to encounter polar temperature fronts. In addition, most

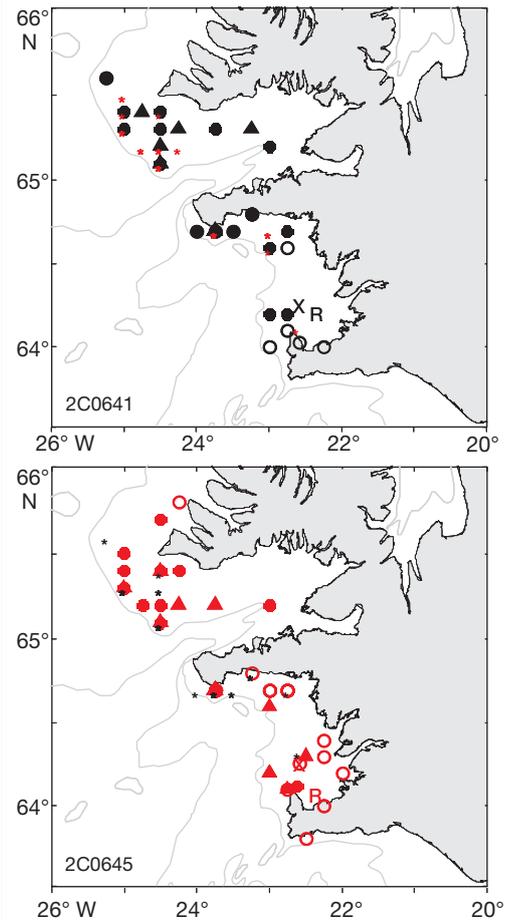


Fig. 4. *Gadus morhua*. Example of geolocation of 2 coastal individuals (2C0641, black; 2C0645, red) which stayed together for 2 yr. Symbols show locations in February to May (○), June to September (▲), October to January (●); location of other individual (*), release (R) and recapture (X) locations

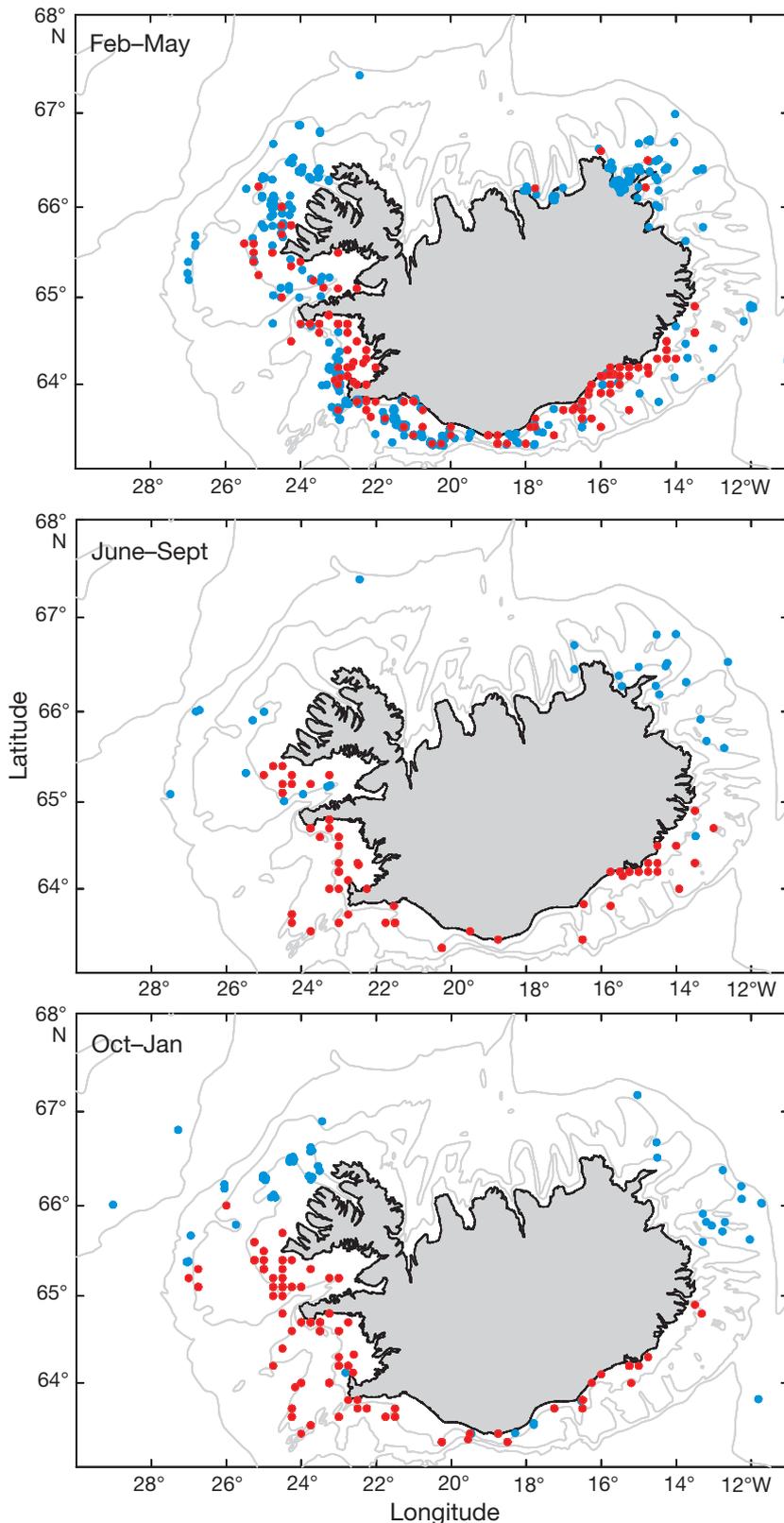


Fig. 5. *Gadus morhua*. Geo-location of individual cod (coastal = red; frontal = blue) based on an improved model of Pedersen et al. (2008). All individuals (41) are presented by regions and seasons

tagged individuals exhibited spawning site fidelity, as they were recaptured at the same GPS location where they were released (data not shown).

DISCUSSION

The development of new tracking methods has provided a unique opportunity to study the spatio-temporal variability of individual migration patterns over more than 1 annual cycle. In this study, using information retrieved from DSTs placed in individual Atlantic cod, the consistency in DSTs profiles, timing of migration and geo-location of coastal and frontal behaviour types over more than 18 mo were investigated for the first time. The results revealed that (1) coastal and frontal behaviour types clearly display distinct seasonal thermobathymetric patterns which are constant from year to year, (2) the onset of migration is consistent from year to year, (3) DST tidal signatures suggest feeding migrations in shoals. These results are the first for Icelandic cod, and each of the above issues is discussed below in more detail.

Although some variation could be observed among regions within types, the 2 behaviour types demonstrated highly consistent and repetitive patterns over the period investigated. Individual coastal cod, moving all year within coastal waters, showed a considerable range in temperatures outside the spawning season, indicating that their feeding habitats may differ in temperature regime within the coastal environment. This also indicates that the coastal cod may travel some distance along the coast during the feeding migrations, a result corroborated by tidal locations of this behaviour type during feeding migrations. On the other hand, the frontal cod migrated out of their spawning grounds at variable temperature and depth, and displayed an extensive, vertical and horizontal

migratory behaviour and a clear separation from the coastal type. Further characteristics of the behaviour of the frontal cod were annual, repeated visits to sub-0 waters, a pattern which was never observed for the coastal type. The results also demonstrate strong, repetitive thermal-bathymetric patterns across 2 or 3 yr. In addition, individuals of both types retained their behaviour characteristic through the observation time, i.e. a coastal type did not demonstrate frontal behaviour patterns or vice versa. Real intermediate characters were not found, although 5 coastal cod were recorded at depth > 200 m in feeding migrations and were classified as intermediates. Those fish nevertheless displayed a temperature history of a coastal cod (Grabowski et al. 2011).

The timing of a migration from spawning to feeding ground and vice versa, which is crucial for individual survival and reproductive success, has been shown to be related either to food availability and temperature (Bell 2011, Schaefer et al. 2011) or to genetic inheritance (Quinn et al. 2000, Pulido et al. 2001). Here, the timing of migrations in 2 successive years was correlated, suggesting a consistency in the onset of migration for each behaviour type. A successful migration strategy would imply the retainment of migratory behaviours for the benefit of reduced food competition (Brodersen et al. 2012). The consistency observed here might reflect successful, concurrent strategies to avoid resource competition within a large, coastal population. A recent stomach content analysis of inshore versus offshore cod, supportive of this hypothesis, showed a frontal cod diet of capelin and the deep-water northern ambereye *Hymenodora glacialis*, a diet unlikely for coastal cod within the feeding season (Jónsdóttir et al. in press). Individual consistency in the timing of migrations, and the destination of winter feeding migrations, has been mentioned for freshwater fish (Brodersen et al. 2012). For marine fish, however, this seems to be the first observation. The direction and timing of feeding or winter migrations have also been shown to be under genetic control in bird populations (Helbig et al. 1994, Pulido et al. 2001) and freshwater fish (Quinn et al. 2000). Both frontal and coastal behaviours exhibit different genotypes at the pantophysin locus (Pampoulie et al. 2008a), which might suggest some genetic basis or at least differences among the 2 behaviour types, but further genetic investigations have to be performed to assess whether the observed migration pattern has a genetic basis. However, the fact that individuals of both types retain their behavioural characteristics through the observation time, i.e. the coastal behaviour type

never changed to the frontal behaviour type or vice versa, tends to suggest that a genetic basis might be responsible for the difference in feeding strategy. In Norwegian waters, differences in the blood type E, the haemoglobin *Hb-I*¹ allele and the *Pan I* locus have led to the suggestion that these cod behaviour types represent sibling species (Møller 1969).

Finally, one of the most striking observations during the present study was that the tidal location model suggested that the feeding migrations of cod in Icelandic waters were undertaken in groups or shoals during the whole year. Shoaling is commonly described as groups of fishes that remain together for social reasons with no implication of structure or function (Pitcher 1983, Pitcher & Parrish 1993). Shoaling, or social transmission of migration routes and homing, has been proposed to explain discrepancies among tagging and genetic data in Icelandic cod (Pampoulie et al. 2008b). One possible explanation for the observed results is therefore that social transmission might enable the rapid transfer of beneficial behavioural traits (feeding migration, homing and timing of the migration) from older spawning cod to new recruits (see 'adopted migrant' hypothesis of McQuinn 1997).

Behaviour types, i.e. groups of individuals within the same stock exhibiting different patterns of migration, are part of the life-history portfolio of a species (Greene et al. 2010, Schindler et al. 2010), yet very little information exists on their consequences for the conservation of exploited marine resources. Behavioural effects on vulnerability to harvest have only been recently investigated (Biro & Post 2008), and revealed that more active and bold fish, for example migratory fish, are likely to be more vulnerable to harvest than sedentary fish (Biro & Post 2008). Therefore, the frontal behaviour is likely to be more vulnerable to fishing pressure than the coastal one, and sustainable fisheries require a more complex management practice than the one currently applied. One of the possibilities to avoid the possible overexploitation of this behaviour type would be to apply quotas on the different fishing gears (fishing at different depth), or quotas to different geographical areas which will be proxy of the depth distribution of the different behaviour types as a precautionary approach.

Determining the mechanisms maintaining these 2 consistent behaviour types remains a challenge, and requires further analyses and studies, but the consistent migration pattern is an interesting evolutionary case to investigate. At present, it is difficult to assess whether these migration patterns have a genetic

basis (inheritance), or imply an 'on-going' ecological speciation due to the use of different food resources (Keller & Seehausen 2012).

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